

A new genus name for pygmy lorises, *Xanthonycticebus* gen. nov. (Mammalia, Primates)

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<http://zoobank.org/AF9D1D54-F1DA-44BD-9F57-47058914BEA7>

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Academic editor: Melissa T.R. Hawkins ♦ Received 10 April 2021 ♦ Accepted 7 March 2022 ♦ Published 23 March 2022

Abstract

Lorisiformes are nocturnal primates from Africa and Asia with four genera, with two (*Arctocebus* and *Loris*), three (*Perodicticus*) and nine (*Nycticebus*) recognised species. Their cryptic lifestyle and lack of study have resulted in an underappreciation of the variation at the species and genus level. There are marked differences between the pygmy slow loris *Nycticebus pygmaeus* and the other *Nycticebus* species and, in the past, several authors have suggested that these may warrant recognition at the generic level. We here combine morphological, behavioural, karyotypical and genetic data to show that these contrasts are, indeed, significantly large and consistent. We propose *Xanthonycticebus* gen. nov. as a new genus name for the pygmy slow lorises and suggest a common name of pygmy lorises. Based on analysis of complete mitochondrial DNA sequences, we calculate the divergence of pygmy from slow lorises at 9.9–10.0%. The median date, calculated for the divergence between *Xanthonycticebus* and *Nycticebus*, is 10.5 Mya (range 4.9–21.0 Mya). *Xanthonycticebus* differs from *Nycticebus* by showing sympatry with other slow loris species, by habitually giving birth to twins, by showing seasonal body mass and whole body coat colour changes (absent in other species living at similar latitudes) and a multi-male, multi-female social system. Pygmy lorises are easily recognisable by the absence of hair on their ears and more protruding premaxilla. *Xanthonycticebus* is threatened by habitat loss and illegal trade despite legal protection across their range and all slow lorises are listed on appendix 1 of CITES. The suggested nomenclatural changes should not affect their legal status.

Key Words

conservation, cytotaxonomy, Lorisidae, Lorisiformes, primate taxonomy, Strepsirrhini

Background

Lorisiformes are a group of nocturnal primates with two genera, *Perodicticus* Bennett, 1831 (three species) and *Arctocebus* Gray, 1863 (two species) occurring in west and equatorial Africa and two, *Loris* É. Geoffroy, 1796 (two species) and *Nycticebus*, É. Geoffroy, 1812 (nine species) occurring in south, east and southeast Asia (Groves 2001; Nekaris 2013; Rowe and Meyers 2016). In west-central Africa, *Perodicticus edwardsi* Bouvier, 1979 and *Arctocebus* occur in sympatry and in eastern Indochina, *Nycticebus bengalensis* (Lacépède, 1800) and *N. pygmaeus* Bonhote, 1907 occur in sympatry. All other species have allopatric distributions.

At a major international conference on nocturnal primates in 1993, Schwartz and Beutel (1995: 189), at a time when only two species of *Nycticebus* were recognised, commented that “*N. coucang* and *N. pygmaeus* are species that are remarkable for their variability”. Since then, a considerable amount of comparative research has been conducted on the slow lorises, including morphologically (e.g. Ravosa 1998; Groves 2001; Nekaris and Jaffe 2007; Munds et al. 2013; Xie et al. 2013 7), behaviourally (e.g. Fitch-Snyder and Ehrlich 2003; Nekaris et al. 2008; Nekaris et al. 2010; Streicher et al. 2012; Ni et al. 2020; Poindexter and Nekaris 2020) and genetically (e.g. Chen et al. 2006; Perelman et al. 2011; Pozzi et al. 2015; Munds et al. 2018; Munds et al. 2021). Combined, these studies

allow us to gain a better understanding of the species and higher-level taxonomy. Recent molecular phylogenetic research has revealed the divergence between genera and between species and, from this, it is evident that one species, the pygmy slow loris *N. pygmaeus* is anomalous. In combination with karyotypical, behavioural and morphological data, this supports the conclusion that this species is best placed in its own genus.

Although under the Code (International Commission on Zoological Nomenclature 1999), Art. 13.1, we are not obliged to provide a description of a new taxon (it would suffice to provide a bibliographic reference to earlier descriptions), we feel that, in this instance, it may be opportune to give a generic diagnosis.

Order Primates Linnaeus, 1758

Suborder Strepsirhini É. Geoffroy Saint-Hilaire, 1812
Family Lorisidae Gray, 1821

Xanthonycticebus gen. nov.
<http://zoobank.org/16F2DB84-82CD-44B9-B9A8-30A8BA64BD20>

Diagnosis. Morphological synapomorphies to *Xanthonycticebus* include: (i) skull length consistently less than 55 mm, (ii) diastema between P² and P³, (iii) long black ears, hairless at the tips (iv) relatively narrow interorbital distance compared to *Nycticebus* and (v) full seasonal coat colour change including almost complete loss of dorsal stripe (Fig. 1). The species is furthermore distinguished from *Nycticebus* species by giving birth habitually to

twins, frequent sympatry with *N. bengalensis* (sensu lato) and more rapid locomotion. Regarding multiple births, this trait occurs with varying frequency in primates. Most of the marmosets and tamarins are polyovulatory and twins are the dominant litter size in the wild and most twins are considered dizygotic (Ward et al. 2014; Wahab et al. 2015). Old World monkeys, apes and humans are monovulatory species and while single births are the rule, multiple births do occasionally occur in various species, typically at a rate at, or below one percent (Geissmann 1990). Around two-thirds to three-quarters of these twins are estimated to be monozygotic (Geissmann 1990). This contrasts with twinning in strepsirrhines, as here all, or practically all, are dizygotic (Pasztor and Van Horn 1979). No other species of slow lorises are known to be sympatric, with their distribution similar to gibbons Hylobatidae Gray, 1870 and langurs Presbytina Gray, 1825, which, even though having more recent evolutionary histories, contain multiple genera (Rowe and Meyers 2016). Where nocturnal primate genera or species are sympatric, different locomotor strategies have evolved, allowing reduced competition (Charles-Dominique 1977). Additional differences, as well as those from *Loris*, are summarised in Table 1.

Etymology. The genus name *Xanthonycticebus*, masculine, refers to the species orange/ish overall colouration and their nocturnal activity pattern; Xanto, Gr. Yellowish-orange; nykt-, Gr., night; kêbos, Gr., monkey (Gainsford 2020). Currently, the most frequently used common name of this genus is pygmy slow loris, followed by the rarely used lesser slow loris or intermediary slow loris. For the common English name, we suggest pygmy loris in order to differentiate the new genus from

Table 1. Summary of key similarities and differences amongst the three Asian lorisiform genera.

	<i>Loris</i>	<i>Nycticebus</i>	<i>Xanthonycticebus</i>	Reference
Latitudinal range	6°N–20°N	8°S–28°N	10°N–25°N	Ravosa (1998)
Altitudinal range (asl)	0–2,000 m	0–2,400 m	50–1,500 m	Nekaris (2013)
Twins	Rare but occasional	Absent or very rare	Habitually	Fitch-Snyder and Ehrlich (2003)
Torpor	Absent	Present	Present	Streicher and Reinhardt (2020)
Venomous	Absent	Present, 68 volatile and semi-volatile components	Present, 200 volatile and semi-volatile components	Hagey et al. (2007)
Seasonal body mass change	Absent	Absent	Present	Streicher (2004)
Seasonal coat colour change	Absent	Dorsal stripe shortens in some species	Full coat and dorsal stripe change	Streicher (2004); Nekaris, unpubl. data.
Species	Two	Nine	One, possibly two	Rowe and Meyers (2016)
Body size, range	120–330 g	265–2200 g	360–580 g	Nekaris (2013)
Ears	Haired, larger than in <i>Nycticebus</i> or <i>Xanthonycticebus</i>	Haired and small often with tufts	Ear length intermediate and naked at tips	Osman Hill (1953)
Multi-male, multi-female social system	Present	Absent	Present	Poindexter and Nekaris (2020)
Gestation	160–170 d	184–197 d	184–200 d	Fitch-Snyder (2020)
Molar size	M ² larger than M ¹	M ¹ larger than M ²	M ² larger than M ¹	Osman Hill (1953)
Karyotype and nucleolus organiser regions (NORs)	2n = 62	2n = 50; NORs on chromosome 1, 6, 9, 15 and 23	2n = 50; NORs on chromosome 6, 9 and 15	Chen et al. (1993); Goonan et al. (1995)
Third hand pad	Smallest	Intermediate or small	Largest	Osman Hill (1953); Nekaris, unpubl. data.
Snout	Narrow and pointy	Broader and more rounded	Broader than <i>Loris</i> , but longer premaxilla than <i>Nycticebus</i>	Osman Hill (1953)
Interorbit	Narrowest	Widest	Intermediate	Ravosa (1998)
Ocular axial and corneal diameter	AD – 14.0 mm; CD – 12.0 mm	AD – 15.7 mm; CD – 12.1 mm	AD – 15.5 mm; CD – 12.3 mm	Ross and Kirk (2007)

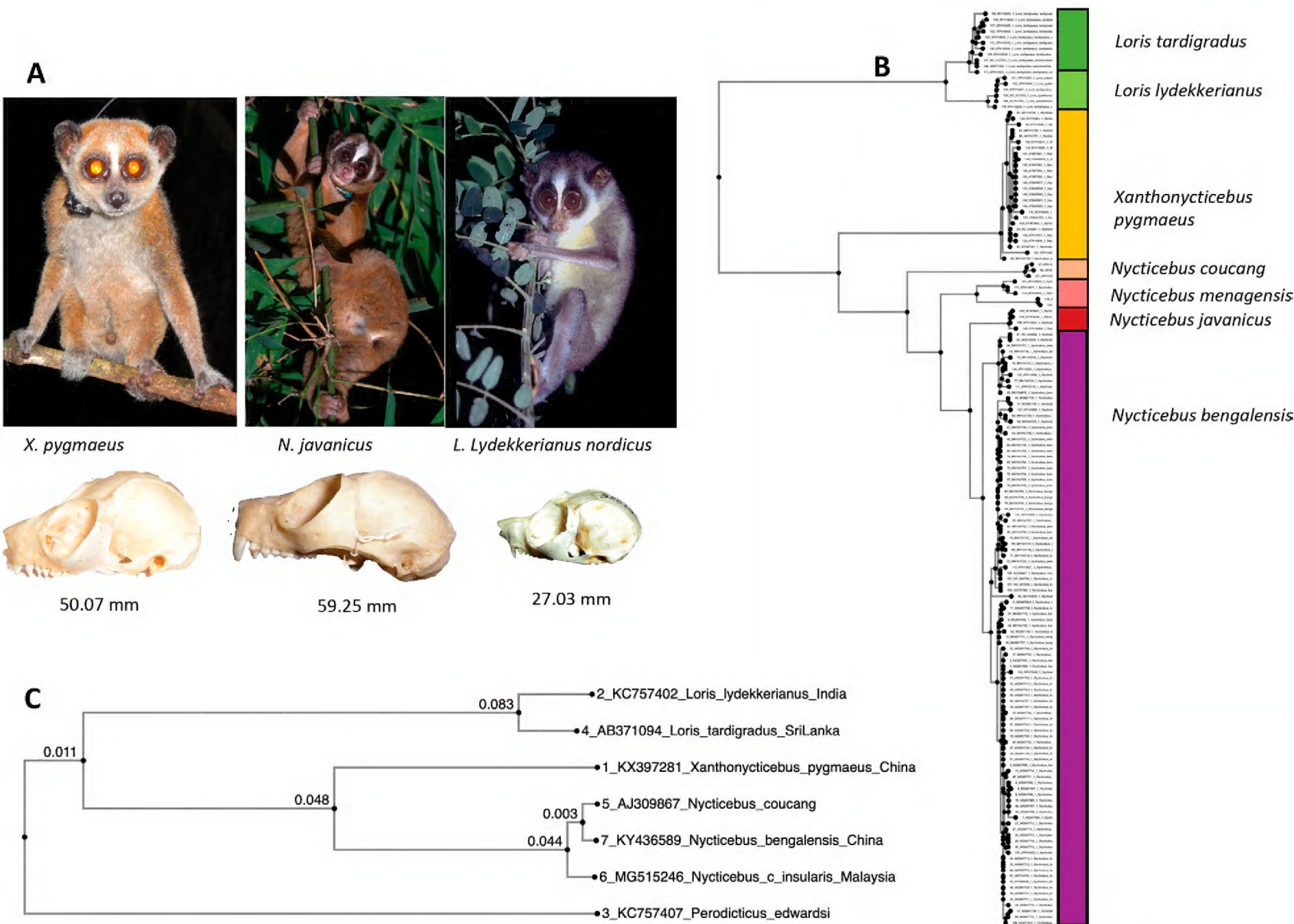


Figure 1. Characteristics of pygmy loris *Xanthonycticebus pygmaeus* gen. nov. **A.** Photograph of wild adult male *X. pygmaeus* from Mondulkiri District, Cambodia and skull from Li Chau, Vietnam (FMNH 32499), compared with *Nycticebus javanicus* from Garut Regency, Indonesia and skull (RMNH14563) from South Java, Indonesia; and with *Loris lydekkerianus nordicus* from Trincomalee District, Sri Lanka and skull (FMNH95029) from Jaffna District, Sri Lanka. Features distinctive to *Xanthonycticebus* include yellowish-orange colour, mid-broad snout with long premaxilla, M^2 larger than M^1 and ears hairless at the tips; **B.** Neighbour-joining tree of 175 cytochrome b sequences (alignment 1,068 bp) of *Nycticebus*, *Xanthonycticebus* and *Loris*; **C.** Neighbour-joining tree of complete mtDNA sequences of *Nycticebus*, *Xanthonycticebus* and *Loris*, with *Perodicticus* as outgroup, showing considerable divergence of *Xanthonycticebus* from *Nycticebus*. All photographs courtesy of K.A.I. Nekaris.

the two other loris genera (slow and slender lorises). We acknowledge, however, that with the recognition of *N. menagensis* Munds, Nekaris and Ford 2013, from Borneo, with a minimum adult body mass of 265 g, the small size is no longer a unique feature of the pygmy loris. The most commonly-used name for pygmy lorises in Vietnamese is Cu li nhỏ, in Mnong, it is Tau kless, in Lao, it is Linh lom and in Chinese, it is 小懶猴 / Xiǎo lǎn hóu (Nijman and Nekaris 2016; Thach et al. 2018).

Contents. a single species, *Xanthonycticebus pygmaeus* (Bonhote, 1907) is currently recognised and *Nycticebus intermedius* Dao Van Tien, 1960 and the not formally described *N. chinensis* are treated as synonyms. There is clear clinal latitudinal variation in body size and craniofacial size (smaller in the north) (Ravosa 1998). Variation in pelage colourations, coupled with a considerable amount of genetic divergence between available sequences deposited in GenBank (e.g. up to 2.0% in *cytb*; Fig. 1), largely from specimens without exact geographic locality data, may lead to the recognition of additional species in the future. Pozzi et al. (2020), based on monophyletic northern and southern populations of pygmy lorises from

Laos PDR, Cambodia and Vietnam, advocate more research to confirm if these are, indeed, two species.

Mein and Ginsburg (1997) tentatively described a single third upper molar M^3 (T Li 41) from Li Mae Long in Lamphum Province, Thailand dated to the early Miocene, 17–18 Mya, as ?*Nycticebus linglom* Mein & Ginsburg, 1997. The small size (1.29×1.82 mm) shows affinities with *X. pygmaeus*, but absence of a hypocone and a metacone on M^3 on T Li 41 aligns it closer to *N. bengalensis* than to *X. pygmaeus* and Li Mae Long is situated west of the Mekong River, outside the current distribution range of *X. pygmaeus*. We suggest to retain ?*Nycticebus linglom* within the genus *Nycticebus*.

The holotype of *X. pygmaeus* is a juvenile male collected by J. Vassal on 13 November 1905 in Nha Trang Vietnam [12.24, 109.19], that is currently stored in the Natural History Museum London under registration number 1906.11.6.2. It is described in detail by Bonhote (1907).

Divergence and molecular clock dates. Several molecular phylogenetic studies have been conducted that included samples of *X. pygmaeus* and two or more other *Nycticebus* species; in all analyses, *X. pygmaeus* is the first

Table 2. Estimates of the timing of the split between *Nycticebus* and *Xanthonycticebus* (in Million years ago, range is expressed as the 95% highest posterior density of divergence time estimates).

Type (bp)	<i>Nycticebus</i> species included in calculation	Split (mean, range), Mya	Reference
Mitochondrial genes			
Cytochrome b (1140)	<i>javanicus</i> / <i>bengalensis</i> / <i>cougang</i> / <i>menagensis</i>	10.9 (7.6–14.5)	Pozzi et al. (2015)
Cytochrome b + cytochrome oxidase subunit 1 (536)	<i>cougang</i>	26.4 (13.1–39.7)	Munds et al. (2018)
Nuclear genes			
18 gene regions (9,500)	<i>cougang</i>	6.4 (3.5–10.1)	Horvath et al. (2008)
54 gene regions (34,927)	<i>bengalensis</i> / <i>cougang</i>	10.2 (5.4–15.1)	Perelman et al. (2011)
Melanocortin 1 receptor (729)	<i>bengalensis</i> / <i>cougang</i>	12.0	Munds et al. (2021)
Recombinant activation gene 2 intron (716)	<i>cougang</i>	14.5 (6.0–24.9)	Munds et al. (2018)
Mitochondrial and nuclear genes			
4 genes (cytb, co1, rag2, MC1R) (1983)	<i>cougang</i>	18.4 (10.2–26.9)	Munds et al. (2018)

group to split, thus forming two distinct reciprocal monophyletic groups. Our own analysis, based on the complete mitochondrial genome sequences of *Xanthonycticebus* (*X. pygmaeus* GenBank Accession #: [KX397281](#)), two species of *Loris* (*L. lydekkerianus* [KC757402](#) from India and *L. tardigradus* [AB371094](#) from Sri Lanka), three *Nycticebus* (*N. bengalensis* [KY436589](#) from China, *N. c. insularis* [MG515246](#) from Malaysia and *N. cougang* [AJ309867](#) from an unknown location) with *P. edwardsi* [KC757407](#) from Cameroon as an outgroup, likewise shows a genetic distance of 9.9–10.0% between *X. pygmaeus* and the three other *Nycticebus* species (Fig. 1).

The divergence time between *X. pygmaeus* and the other *Nycticebus* species was estimated at between 6.4 Mya and 26.4 Mya (Table 2). Pozzi et al. (2015) commented that the gap of around six million years between the divergence of *X. pygmaeus* and the radiation of the other *Nycticebus* species may lend support to the distinction of *X. pygmaeus* at the generic level. Using data from Perelman et al. (2011), it is evident that the split between *Nycticebus* and *Xanthonycticebus*, by them estimated at 10.2 Mya (95% CI range 5.4–15.1 Mya), considerably predates several widely acknowledged generic splits within the Order Primates, including those between geladas *Theropithecus gelada* and baboons *Papio* spp. / mangabays *Lophocebus* (4.1 Mya; 3.4–4.7 Mya), between *Semnopithecus* and *Trachypithecus* langurs (4.1 Mya; 2.9–5.4 Mya), between *Mico* and *Cebuella* marmosets (4.8 Mya; 2.9–7.2 Mya) and, indeed, between humans *Homo* and chimpanzees / bonobos *Pan* spp. (6.6 Mya; 3.4–7.7 Mya). Estimates of the split between the two genera, based on other genes, nuclear, mitochondrial or both, are generally between 10 and 20 Mya, with some estimates exceeding 25 Mya (Table 2). Thus, in all likelihood, the *Nycticebus* and *Xanthonycticebus* split occurred by the Late to Middle Miocene and possibly as early as the Oligocene.

Even the lower estimates of the divergence between *Nycticebus* and *Xanthonycticebus*, of around 8 Mya pre-date many acknowledged generic splits in a wide range of mammalian taxa. This includes, for instance, those within the Muridae (e.g. *Beamys-Cricetomys*, *Parotomys-Arvicanthis*, *Microtus-Clethrionomys*, *Phyllotis-Calomys* and *Rhipidomys-Phyllotis/Calomys*) (Steppan et al. 2004) and the Cetartiodactyla (e.g. *Capra-Pseudois*, *Ovis-Nilgiritragus*, *Oryx-Addax*, *Bos-Bison*, *Cervus-Rusa* and *Mazama-Odocoileus*) (Zurano et al. 2019). The same is true for other vertebrates, such as birds (e.g. babblers, white-eyes

and bee hummingbirds: Cai et al. 2017; Licona-Vera and Ornelas 2017).

The marked difference between *Nycticebus* and *Xanthonycticebus* is also supported by hybridisation events. In captivity, hybrids (confirmed and suspected) have been recorded between *N. bengalensis* and *N. cougang* and *N. cougang* and *N. hilleri* (other *Nycticebus* species are rarely kept in zoological facilities). Despite being the most common of the slow lorises in captive settings – the Zoological Information Management System lists globally 191 *Xanthonycticebus* and 220 of four other slow loris species combined – there are no records of hybrids between *Xanthonycticebus* and any of the other species. Both *Nycticebus* and *Xanthonycticebus* have n = 50 chromosomes, but karyotypically, the former differs from the latter by having a secondary construction in the short arm of chromosome 1 and the additional presence of nucleolus organiser regions on chromosome pair 1 and 23 (Stanyon et al. 1987; Chen et al. 1993).

Status. *Xanthonycticebus pygmaeus* occurs naturally in Vietnam (historically south to the vicinity of Ho Chi Minh City [10.75, 106.66]), Laos PDR (west to Phongsali [21.59, 102.25]), Cambodia (east of the Mekong River), China (historically north to Lüchun County [23.00, 104.67]) (Nekaris 2013). The species may have established itself in Thailand, west of the Mekong River, as a result of poorly planned release efforts (Osterberg and Nekaris 2015). *Xanthonycticebus pygmaeus* has been assessed as Endangered according to IUCN Red List Criteria, with the trade for medicinal purposes and as pets and habitat loss recognised as the main threats (Starr et al. 2011; Blair et al. 2020). The species is protected in all four of its range countries, but active enforcement of these laws is far from optimal (Nekaris and Starr 2015; Thạch et al. 2018; Ni et al. 2020). The species is the most common loris kept in accredited zoological collections (i.e. 43 in N America, 86 in Europe, 62 in Asia; Species360 2021). In addition, rescue centres in Vietnam, Laos, Thailand, China, United Arab Emirates and Japan have at least 79 individuals under their care (e.g. Kenyon et al. 2014; Khudamrongsawat et al. 2018; Yamanashi et al. 2021). The species is part of both American Zoo Association and European Association of Zoos and Aquariums breeding programmes, but birth rates are low.

The genus *Nycticebus* is listed in appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), precluding all commercial international trade (Nekaris and Nijman 2007).

In the proposal, submitted by Cambodia in 2007, which was accepted by consensus, three species names were singled out, including *Nycticebus pygmaeus* (with *N. intermedius* and *N. chinensis* listed as synonyms). As such, with respect to international trade, there is no doubt that *Xanthonycticebus* gen. nov. continues to receive the same level of protection and regulation as other slow lorises.

Acknowledgements

We thank the following museums and staff for access to specimens under their care: Colombo Natural History Museum, Field Museum of Natural History-Chicago, Naturalis Leiden, Zoological Museum Amsterdam (now merged with Naturalis), Natural History Museum London and Natural History Museum Oxford. Funding was received from the Systematics Research Fund of the Linnean Society, The Royal Society and SYNTHESIS Project, financed by the European Community Research Infrastructure Action under the FP6 Structuring the European Research Area programme (NL-TAF 3491). Our long-term field projects on slow and slender lorises in Sri Lanka, Cambodia and Indonesia has been supported by People's Trust for Endangered Species, Cleveland Zoological Society and Cleveland Metroparks Zoo and Disney Worldwide Conservation Fund. We thank Aconk Ahmad, Penelope Goodman, Zak Showell, Carly Starr and Ariana Weldon for support and three reviewers and the editor for constructive comments and suggestions for improvement.

References

- Blair M, Nadler T, Ni O, Samun E, Streicher U, Nekaris KAI (2020) *Nycticebus pygmaeus*. The IUCN Red List of Threatened Species 2020: e.T14941A17971417. <https://doi.org/10.2305/IUCN.UK.2020-2.RLTS.T14941A17971417.en> [Downloaded on 17 March 2021]
- Bonhote JL (1907) On a collection of mammals made by Dr Vassal in Annam. Proceedings of the Zoological Society of London 1907(1): 3–11. <https://doi.org/10.1111/j.1096-3642.1907.tb01797.x>
- Charles-Dominique P (1977) Ecology and behaviour of nocturnal primates: Prosimians of Equatorial West Africa. Columbia University Press, New York.
- Cai T, Cibois A, Alström P, Moyle RG, Kennedy JD, Shao S, Zhang R, Irestedt M, Ericson PG, Gelang M, Qu Y (2019) Near-complete phylogeny and taxonomic revision of the world's babblers (Aves: Passeriformes). Molecular Phylogenetics and Evolution 130: 346–356. <https://doi.org/10.1016/j.ympev.2018.10.010>
- Chen Z, Zhang Y, Shi L, Liu R, Wang Y (1993) Studies on the chromosomes of genus *Nycticebus*. Primates 34(1): 47–53. <https://doi.org/10.1007/BF02381279>
- Chen JH, Pan D, Groves C, Wang YX, Narushima E, Fitch-Snyder H, Crow P, Thanh VN, Ryder O, Zhang HW, Fu YX, Zhang Y (2006) Molecular phylogeny of *Nycticebus* inferred from mitochondrial genes. International Journal of Primatology 27(4): 1187–1200. <https://doi.org/10.1007/s10764-006-9032-5>
- Fitch-Snyder H (2020) Husbandry and reproductive management recommendations for captive lorises and pottos (*Nycticebus*, *Loris* and *Perodicticus*). In: Nekaris KAI, Burrows A (Eds) Evolution, ecology and conservation of lorises and pottos (Cambridge studies in biological and evolutionary anthropology). Cambridge University Press, Cambridge, 263–276. <https://doi.org/10.1017/9781108676526.026>
- Fitch-Snyder H, Ehrlich A (2003) Mother-infant interactions in slow lorises (*Nycticebus bengalensis*) and pygmy lorises (*Nycticebus pygmaeus*). Folia Primatologica 74(5–6): 259–271. <https://doi.org/10.1159/000073313>
- Gainsford P (2020) How to make sense of ancient Greek colours. Kiwi Hellenist. [Accessed on 9 April 2021] <http://kiwihellenist.blogspot.com/2020/05/ancient-greek-colours.html>
- Geissmann T (1990) Twinning frequency in catarrhine primates. Human Evolution 5(4): 387–396. <https://doi.org/10.1007/BF02437252>
- Goonan PM, Groves CP, Smith RD (1995) Karyotype polymorphism in the slender loris (*Loris tardigradus*). Folia Primatologica 65(2): 100–109. <https://doi.org/10.1159/000156874>
- Groves CP (2001) Primate Taxonomy. Smithsonian Press, Washington.
- Hagey LR, Fry BG, Fitch-Snyder H (2007) Talking defensively, a dual use for the brachial gland exudates of slow and pygmy lorises. In: Gursky SL, Nekaris KAI (Eds) Primate anti-predator strategies. Springer, New York, 253–272. https://doi.org/10.1007/978-0-387-34810-0_12
- Horvath JE, Weisrock DW, Embry SL, Fiorentino I, Balhoff JP, Kappeler P, Wray GA, Willard HF, Yoder AD (2008) Development and application of a phylogenomic toolkit: Resolving the evolutionary history of Madagascar's lemurs. Genome Research 18(3): 489–499. <https://doi.org/10.1101/gr.7265208>
- ICZN (1999) International Code of Zoological Nomenclature. Fourth Edition. The International Trust for Zoological Nomenclature, London.
- Kenyon M, Streicher U, Loung H, Tran T, Tran M, Vo B, Cronin A (2014) Survival of reintroduced pygmy slow loris *Nycticebus pygmaeus* in South Vietnam. Endangered Species Research 25(2): 185–195. <https://doi.org/10.3354/esr00607>
- Khudamrongsawat J, Nakchamnan K, Laithong P, Kongrit C (2018) Abnormal repetitive behaviours of confiscated slow lorises (*Nycticebus* spp.) in Thailand. Folia Primatologica 89(3–4): 216–223. <https://doi.org/10.1159/000487432>
- Licona-Vera Y, Ornelas JF (2017) The conquering of North America: dated phylogenetic and biogeographic inference of migratory behavior in bee hummingbirds. BMC Evolutionary Biology 17(1): 1–17. <https://doi.org/10.1186/s12862-017-0980-5>
- Mein P, Ginsburg L (1997) Les mammifères du gisement miocène inférieur de Li Mae Long, Thaïlande: Systématique, biostratigraphie et paléoenvironnement. Geodiversitas 19: 783–844.
- Munds RA, Nekaris KAI, Ford SM (2013) Taxonomy of the Bornean slow loris, with new species *Nycticebus kayan* (Primates, Lorisidae). American Journal of Primatology 75(1): 46–56. <https://doi.org/10.1002/ajp.22071>
- Munds RA, Titus CL, Eggert LS, Blomquist GE (2018) Using a multi-gene approach to infer the complicated phylogeny and evolutionary history of lorises (Order Primates: Family Lorisidae). Molecular Phylogenetics and Evolution 127: 556–567. <https://doi.org/10.1016/j.ympev.2018.05.025>
- Munds RA, Titus CL, Moreira LA, Eggert LS, Blomquist GE (2021) Examining the molecular basis of coat color in a nocturnal primate family (Lorisidae). Ecology and Evolution 11(9): 4442–4459. <https://doi.org/10.1002/ece3.7338>
- Nekaris KAI (2013) Lorisidae. In: Mittermeier RA, Rylands AB, Wilson DE (Eds) Handbook of the Mammals of the World: 3. Primates. Lynx Ediciones, Barcelona, 210–235.

- Nekaris KAI, Jaffe S (2007) Unexpected diversity of slow lorises (*Nycticebus* spp.) within the Javan pet trade: Implications for slow loris taxonomy. *Contributions to Zoology* (Amsterdam, Netherlands) 76(3): 187–196. <https://doi.org/10.1163/18759866-07603004>
- Nekaris KAI, Nijman V (2007) CITES proposal highlights rarity of Asian nocturnal primates (Lorisidae, *Nycticebus*). *Folia Primatologica* 78(4): 211–214. <https://doi.org/10.1159/000102316>
- Nekaris KAI, Starr CR (2015) Conservation and ecology of the neglected slow loris: Priorities and prospects. *Endangered Species Research* 28(1): 87–95. <https://doi.org/10.3354/esr00674>
- Nekaris KAI, Blackham GV, Nijman V (2008) Conservation implications of low encounter rates of five nocturnal primate species (*Nycticebus* spp.) in Asia. *Biodiversity and Conservation* 17(4): 733–747. <https://doi.org/10.1007/s10531-007-9308-x>
- Nekaris KAI, Starr CR, Collins RL, Wilson A (2010) Comparative ecology of exudate feeding by lorises (*Nycticebus*, *Loris*) and pottos (*Perodicticus*, *Arctocebus*). In: Burrows A, Nash LT (Eds) *The Evolution of Exudativory in Primates*. Springer, New York, 155–168. https://doi.org/10.1007/978-1-4419-6661-2_8
- Ni Q, He X, Wang Y, Meng X (2020) Distribution and conservation status of slow lorises in Indo-China. In: Nekaris KAI, Burrows A (Eds) *Evolution, ecology and conservation of lorises and pottos* (Cambridge studies in biological and evolutionary anthropology). Cambridge University Press, Cambridge, 326–338. <https://doi.org/10.1017/9781108676526.032>
- Nijman V, Nekaris KAI (2016) Provide context when reporting on the use of protected and endangered wildlife in ethnopharmacological surveys. *Journal of Ethnopharmacology* 194: 577–579. <https://doi.org/10.1016/j.jep.2016.10.066>
- Osman-Hill WC (1953) *Primates: A comparative anatomy and taxonomy*. I-Strepsirhini. Edinburgh University Press, Edinburgh.
- Osterberg P, Nekaris KAI (2015) The use of animals as photo props to attract tourists in Thailand: A case study of the slow loris *Nycticebus* spp. *Traffic Bulletin* 27: 13–18.
- Pasztor LM, Van Horn RN (1979) Twinning. In: Andrews EJ, Ward BC, Altman NH (Eds) *Spontaneous Animal Models of Human Disease*, Vol. I. Academic Press, New York, 227–230.
- Perelman P, Johnson WE, Roos C, Seuánez HN, Horvath JE, Moreira MA, Kessing B, Pontius J, Roelke M, Rumpler Y, Schneider MPC, Silva A, O'Brien SJ, Pecon-Slattery J (2011) A molecular phylogeny of living primates. *PLOS Genetics* 7(3): e1001342. <https://doi.org/10.1371/journal.pgen.1001342>
- Poindexter S, Nekaris KAI (2020) The evolution of social organisation in Lorisiformes. In: Nekaris KAI, Burrows A (Eds) *Evolution, ecology and conservation of lorises and pottos* (Cambridge studies in biological and evolutionary anthropology). Cambridge University Press, Cambridge, 129–137. <https://doi.org/10.1017/9781108676526.012>
- Pozzi L, Nekaris KAI, Perkin A, Bearder SK, Pimley ER, Schulze H, Streicher U, Nadler T, Kitchener A, Zischler H, Zinner D, Roos C (2015) Remarkable ancient divergences amongst neglected lorisiform primates. *Zoological Journal of the Linnean Society* 175(3): 661–674. <https://doi.org/10.1111/zoj.12286>
- Pozzi L, Roos C, Blair ME (2020) Molecular advances in lorisid taxonomy and phylogeny. In: Nekaris KAI, Burrows A (Eds) *Evolution, ecology and conservation of lorises and pottos* (Cambridge studies in biological and evolutionary anthropology). Cambridge University Press, Cambridge, 57–66. <https://doi.org/10.1017/9781108676526.007>
- Ravosa MJ (1998) Cranial allometry and geographic variation in slow lorises (*Nycticebus*). *American Journal of Primatology* 45(3): 225–243. [https://doi.org/10.1002/\(SICI\)1098-2345\(1998\)45:3%3C225::AID-AJP1%3E3.0.CO;2-Y](https://doi.org/10.1002/(SICI)1098-2345(1998)45:3%3C225::AID-AJP1%3E3.0.CO;2-Y)
- Ross CF, Kirk EC (2007) Evolution of eye size and shape in primates. *Journal of Human Evolution* 52(3): 294–313. <https://doi.org/10.1016/j.jhevol.2006.09.006>
- Rowe N, Meyers M (2016) *All the world's primates*. Pogonias Press, Charlestown, USA.
- Schwartz JH, Beutel JC (1995) Species diversity in lorisids: a preliminary analysis of *Arctocebus*, *Perodicticus* and *Nycticebus*. In: Altermann L, Doyle GA, Izard MK (Eds) *Creatures of the dark. The nocturnal prosimians*. Plenum Press, New York, 171–192. https://doi.org/10.1007/978-1-4757-2405-9_12
- Species360 (2021) Zoological Information Management System (ZIMS). <https://zims.species360.org>
- Stanyon R, Masters JC, Romagno D (1987) The chromosomes of *Nycticebus coucang* (Boddaert, 1785) (Primates: Prosimii). *Genetica* 75(2): 145–152. <https://doi.org/10.1007/BF00055258>
- Starr C, Nekaris KAI, Streicher U, Leung LKP (2011) Field surveys of the Vulnerable pygmy slow loris *Nycticebus pygmaeus* using local knowledge in Mondulkiri Province, Cambodia. *Oryx* 45(1): 135–142. <https://doi.org/10.1017/S0030605310001316>
- Steppan SJ, Adkins RM, Anderson J (2004) Phylogeny and divergence-date estimates of rapid radiations in muroid rodents based on multiple nuclear genes. *Systematic Biology* 53(4): 533–553. <https://doi.org/10.1080/10635150490468701>
- Streicher U (2004) Aspects of ecology and conservation of the pygmy loris *Nycticebus pygmaeus* in Vietnam. PhD thesis, Ludwig-Maximilians-Universität München, Germany.
- Streicher U, Reinhardt K (2020) Thermoregulation in lorises. In: Nekaris KAI, Burrows A (Eds) *Evolution, ecology and conservation of lorises and pottos* (Cambridge studies in biological and evolutionary anthropology). Cambridge University Press, Cambridge, 187–192. <https://doi.org/10.1017/9781108676526.018>
- Streicher U, Wilson A, Collins RL, Nekaris KAI (2012) Exudates and animal prey characterize slow loris (*Nycticebus pygmaeus*, *N. coucang* and *N. javanicus*) diet in captivity and after release into the wild. In: Masters J, Genin F, Crompton R (Eds) *Leaping ahead: Advances in prosimian biology*. Springer, New York, 165–172. https://doi.org/10.1007/978-1-4614-4511-1_19
- Thạch HM, Le MD, Vũ NB, Panariello A, Sethi G, Sterling EJ, Blair ME (2018) Slow loris trade in Vietnam: Exploring diverse knowledge and values. *Folia Primatologica* 89(1): 45–62. <https://doi.org/10.1159/000481196>
- Wahab F, Drummer C, Behr R (2015) Marmosets. *Current Biology* 25(18): 780–782. <https://doi.org/10.1016/j.cub.2015.06.042>
- Ward JM, Buslov AM, Vallender EJ (2014) Twinning and survivorship of captive common marmosets (*Callithrix jacchus*) and cotton-top tamarins (*Saguinus oedipus*). *Journal of the American Association for Laboratory Animal Science*, JAALAS 53: 7–11.
- Xie ZH, Hu JY, Zhou MY, Deng DJ (2013) Characteristics of the limb in slow loris and pygmy loris. *Chinese Journal of Anatomy* 36: 405–407.
- Yamanashi Y, Nemoto K, Alejandro J (2021) Social relationships among captive male pygmy slow lorises (*Nycticebus pygmaeus*): Is forming male same-sex pairs a feasible management strategy? *American Journal of Primatology* 83(2): a23233. <https://doi.org/10.1002/ajp.23233>
- Zurano JP, Magalhães FM, Asato AE, Silva G, Bidau CJ, Mesquita DO, Costa GC (2019) Cetartiodactyla: Updating a time-calibrated molecular phylogeny. *Molecular Phylogenetics and Evolution* 133: 256–262. <https://doi.org/10.1016/j.ympev.2018.12.015>